

Age- and nutrition-related cannibalism in larvae of the cotton bollworm, *Helicoverpa armigera* (Lepidoptera: Noctuidae)

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Abstract: 【Aim】Cannibalism could facilitate the infection of certain pathogens that can be transmitted by feeding on infected conspecifics. This may have potential applications in the control of pests by entomopathogens. Our study aims to explore the relation between cannibalism and age and nutrition in larvae of the cotton bollworm, *Helicoverpa armigera*. 【Methods】We estimated the incidence of cannibalism of *H. armigera* larvae by feeding different concentrations of sodium to a laboratory population and a wild population, and examined whether dietary sodium had any effects on the cannibalism. 【Results】The survival rates of the larvae of *H. armigera* were the lowest when the tests were initiated at the beginning of the 3rd and 4th instars, statistically significantly increased when the experiments were carried out at the beginning of the 5th instar, and further raised when the experiments were performed at the beginning of the 6th instar. Moreover, the survival rates of the larvae fed on normal diet prior to experiment were the highest, and slightly but distinctly decreased when the larvae fed on sodium-deficient diet. In addition, the pupation rates of the larvae were similar, irrespective of whether the larvae fed on normal or sodium-deficient diets, and whether the experiments initiated at the beginning of the 3rd, 4th, 5th or 6th instar. 【Conclusion】The results demonstrate that for *H. armigera* larvae cannibalism highly occurs in the 4th and 5th instars rather than the 3rd and 6th instars, and to some extent, sodium deficiency enhances cannibalism. This study provides a basis for further work in this field.

Key words: *Helicoverpa armigera*; larva; cannibalism; larval instar; nutrition; sodium

1 INTRODUCTION

Entomopathogens form the basis for many biological insecticides with proven commercial potential (Moscardi, 1999). However, a major factor that limits their effects is the transmission of these insect pathogens among individuals. Cannibalism, or intraspecific predation, is a widespread phenomenon in Insecta (Elvira *et al.*, 2010; Richardson *et al.*, 2010; Rudolf *et al.*, 2010), especially in Lepidoptera (Williams and Hernández, 2006), which included 48 species in 15 families (Richardson *et al.*, 2010). Cannibalism has been reported as a viable route of horizontal transmission of these insect pathogens. It was found that the 5th instar larvae of several lepidopteran species fed equally on healthy larvae, virus-infected larvae, uninfected corpses, and virus-killed corpses

(Dhandapani *et al.*, 1993; Vasconcelos, 1996; Boots, 1998; Chapman *et al.*, 1999b). This demonstrated that the larvae were unable to detect and avoid infected conspecifics. As a result, this cannibalistic behavior led to the horizontal transmission of several pathogen viruses in natural and laboratory populations of several lepidopteran species, including nucleopolyhedroviruses in *Helicoverpa armigera* (Hübner) (Dhandapani *et al.*, 1993), *Mamestra brassicae* (Vasconcelos, 1996) and *Spodoptera frugiperda* (Chapman *et al.*, 1999b), granulovirus in *Plodia interpunctella* (Boots, 1998), and an iridescent virus of *S. frugiperda* (Williams and Hernández, 2006). Therefore, cannibalism behavior may have potential applications in the control of pests by entomopathogens to meet economic, public health, and environmental goals.

Cannibals in Lepidoptera were usually

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juveniles, possibly because mouthparts of most lepidopteran adults are unsuitable for predation (Richardson *et al.*, 2010), and often consume eggs (Sigsgaard *et al.*, 2002) and other juveniles (Boots, 1998; Kakimoto *et al.*, 2003). The frequency of cannibalism increased with increasing density (Chapman *et al.*, 1999b; Elvira *et al.*, 2010) and decreasing food quantity or quality (Vasconcelos, 1996; Chapman *et al.*, 1999b). Moreover, the incidence of cannibalism was clearly affected by the age of the individuals involved (Chapman *et al.*, 1999b; Elvira *et al.*, 2010). In addition, infected larvae may become less vigorous and therefore less capable of defending themselves than uninfected larvae, and hence more likely to become the victims of cannibals (Poprawski and Yule 1990; Boots, 1998).

The cotton bollworm, *H. armigera*, is a highly polyphagous agricultural pest throughout much of its distribution in tropical and subtropical region of the Old World. In China, the adults would likely to lay eggs in masses on cotton plants (Xu *et al.*, 2006; Liu *et al.*, 2008), which actually increases the chances that conspecifics will encounter one another. The larvae dispersed when they reached high larval density and eventually exhibited a uniform spatial distribution. Moreover, the larvae also frequently attack and then consume conspecific eggs and other juveniles (Sigsgaard *et al.*, 2002; Kakimoto *et al.*, 2003). The cannibals' fitness of *H. armigera* decreased under suitable food conditions, whereas larvae with a low frequency of cannibalism increased their pupal weight in unsuitable conditions (Kakimoto *et al.*, 2003). Moreover, *H. armigera* larvae fed on sodium-deprived artificial diet exhibited much more significant tendency in eating conspecific cadaver (Xiao *et al.*, 2010).

To the best of our knowledge, the influence of age on the incidence of cannibalism was not tested in *H. armigera* larvae. Moreover, in the study on the influence of sodium-deficient artificial diet on the incidence of cannibalism, the authors freshly incapacitated the victims by rupture of the head capsule to make them unable to injure cannibals (Xiao *et al.*, 2010). This result does not reflect the actual cannibalism in natural cotton fields. The purpose of this study was to clarify the relation between cannibalism and age and nutrition in larval *H. armigera*. We found that cannibalism highly occurred in the 4th and 5th instars rather than the 3rd and 6th instars, sodium deficiency slightly but distinctly enhanced cannibalism, and neither

cannibalism nor sodium deficiency exhibited effects on population rates.

2 MATERIALS AND METHODS

2.1 Test insects

H. armigera larvae of the laboratory population were collected from cotton plants (*Gossypium hirsutum*) at Jingzhou city (30.0°N, 114.1°E), Hubei province in China in July 1993. The laboratory population was routinely reared in an insectary under controlled temperature ($28 \pm 1^\circ\text{C}$), photoperiod (14L : 10D) and relative humidity (70% – 80%) according to the method described previously (Xu *et al.*, 2006; Liu *et al.*, 2008) since then. The wild population were also collected from cotton plants (*G. hirsutum*) at Jingzhou city (30.0°N, 114.1°E), Hubei province in China in August 2010. The eggs were cultured till the 3rd, 4th, 5th or 6th instars and the resulting larvae were directly used in experiment. The artificial diet used here was the same as that applied by Xiao *et al.* (2010), only the components of sodium chloride (NaCl) and sodium fluoride (NaF) provided sodium to larvae.

2.2 Cannibalism test

According to Xiao *et al.* (2010), three larval artificial diets differing in sodium concentrations were prepared. Diet A was a conventional diet. Diet B was modified from the conventional diet in which half amounts of sodium chloride (NaCl) and sodium fluoride (NaF) in Wesson salt mixture were replaced with equal mole of potassium chloride (KCl) and potassium fluoride (KF), respectively. Diet C was modified from the conventional diet in which all NaCl and NaF in Wesson salt mixture were replaced with equal moles of KCl and KF, respectively.

Between 12 and 24 h prior to egg hatching, one of the three diets was offered. Since cannibalism rarely occurred in the 1st and 2nd instar larvae of the two *H. armigera* populations when fed on the artificial diet according to our preliminary observation, the resulting larvae at the beginning of the 3rd, 4th, 5th and 6th instars were selected to test the incidence of cannibalism. Larval instars were diagnosed by the head capsule width of larvae, and only the newly molted larvae were used. Six replicates of ten larvae were respectively confined in a petri dish (10 cm in diameter) with respective artificial diet. Larval survival was verified when the larvae reached the prepupal stage.

2.3 Data statistics

The survival rates and pupation rates were given

as mean $\pm SE$, and were arcsine square-root transformed to correct for a slightly non-normal distribution. The data were subjected to one- or two-way analysis of variances (ANOVAs), and followed by Tukey’s test for multiple comparisons at $P < 0.05$ and $P < 0.01$. All statistical data were analyzed using SPSS software (SPSSInc., Chicago, IL, U. S. A.).

3 RESULTS

3.1 The cannibalism of different instars of *H. armigera* larvae

The larvae were first fed on diet A, B or C and subsequently confined in petri dishes with respective artificial diet, the survival rates at the prepupal stage were calculated. Two-way ANOVAs revealed that there were significant differences in the survival rates among different instars when the tests were initiated, but not between the tested populations and the interaction between instar and population (Tables 1 and 2).

Table 1 The survival rates (%) of *Helicoverpa armigera* larvae fed on diets A, B or C prior to experiments and confined together during tests at the beginning of the 3rd, 4th, 5th and 6th instars

Population	Instar	On diet A	On diet B	On diet C
Laboratory	3rd	53 \pm 5 A	51 \pm 6 A	50 \pm 8 A
	4th	60 \pm 7 A	57 \pm 4 A	48 \pm 3 A
	5th	88 \pm 3 B	83 \pm 2 B	79 \pm 4 B
	6th	98 \pm 2 C	98 \pm 2 C	95 \pm 2 C
Wild	3rd	61 \pm 6 A	48 \pm 3 A	47 \pm 6 A
	4th	59 \pm 5 A	53 \pm 4 A	39 \pm 3 A
	5th	70 \pm 5 B	72 \pm 4 B	74 \pm 9 B
	6th	97 \pm 2 C	93 \pm 2 C	97 \pm 2 C

Data in the table are represented as mean $\pm SE$. Different capital letters following the data in the same column indicate significant difference at the 0.01 level (Tukey’s test).

Table 3 One-way ANOVAs for the survival rates in *Helicoverpa armigera* larvae from laboratory and wild populations fed on diets A, B or C prior to experiments

Source	Laboratory population				Wild population			
	<i>d.f.</i>	<i>MS</i>	<i>F</i>	<i>P</i>	<i>d.f.</i>	<i>MS</i>	<i>F</i>	<i>P</i>
A. At the beginning of the 3rd instar								
Survival rate	2	0.0020	0.0778	>0.05	2	0.0439	3.8509	<0.05
Error	15	0.0262			15	0.0114		
Total	17				17			
B. At the beginning of the 4th instar								
Survival rate	2	0.0435	3.6864	<0.05	2	0.0693	6.9300	<0.01
Error	15	0.0118			15	0.0100		
Total	17				17			
C. At the beginning of the 5th instar								
Survival rate	2	0.0242	1.4700	>0.05	2	0.0257	0.4944	>0.05
Error	15	0.0165			15	0.0520		
Total	17				17			
D. At the beginning of the 6th instar								
Survival rate	2	0.0230	1.0526	>0.05	2	0.0230	0.8333	>0.05
Error	15	0.0219			15	0.0276		
Total	17				17			

Table 2 Two-way ANOVAs for the survival rates in *Helicoverpa armigera* larvae confined together at the beginning of the 3rd, 4th, 5th and 6th instars

Source	<i>d.f.</i>	<i>MS</i>	<i>F</i>	<i>P</i>
A. Larvae fed on diet A				
Instar (a)	3	1.0177	44.5518	<0.01
Population (b)	1	0.0403	1.7621	>0.05
a \times b	3	0.0635	2.7818	>0.05
Error	40	0.0228		
Total	47			
B. Larvae fed on diet B				
Instar (a)	3	1.0641	77.7882	<0.01
Population (b)	1	0.0969	7.0833	>0.05
a \times b	3	0.0130	0.9497	>0.05
Error	40	0.0137		
Total	47			
C. Larvae fed on diet C				
Instar (a)	3	1.3420	40.2383	<0.01
Population (b)	1	0.0029	0.0862	>0.05
a \times b	3	0.0123	0.3696	>0.05
Error	40	0.0334		
Total	47			

The survival rates of the larvae fed on diet A, B or C showed similar variation patterns; being the lowest when the tests were initiated at the beginning of the 3rd and 4th instars, statistically significantly increasing when the experiments were carried out at the beginning of the 5th instar, and further raising when the experiments were performed at the beginning of the 6th instar. These data demonstrated that cannibalism highly occurred in the 4th and 5th instars rather than the 3rd and 6th instars (Tables 1 and 2).

3.2 The cannibalism of *H. armigera* larvae when fed on different dietary sodium

One-way ANOVAs were performed to analyze the differences of the survival rates among different diet on which the larvae were fed prior to the experiments (Table 3).

In both tested populations, the survival rates of the larvae fed on diet A were generally the highest. The survival rates of larvae of the laboratory population fed on diet B and C statistically significantly decreased when the test initiated at the beginning of the 4th instar. Similarly, the survival rates of larvae of the wild population fed on diet B and C sharply reduced when the test initiated at the beginning of the 3rd instar, and that of larvae fed on diet C significantly declined when the test initiated at the beginning of the 3rd instar (Tables 1 and 3).

3.3 Influences of cannibalism and dietary sodium on pupation of *H. armigera*

One-way ANOVAs were performed to analyze the influences of cannibalism and dietary sodium on pupation. It was found that the pupation rates of the larvae were similar, irrespective of whether the larvae fed on diet A, B or C prior to experiment, and whether the experiments initiated at the beginning of the 3rd, 4th, 5th or 6th instar (Table 4).

Table 4 The pupation rates (%) of *Helicoverpa armigera* larvae fed on diets A, B or C prior to experiments and confined together during tests at the beginning of the 3rd, 4th, 5th and 6th instars

Population	Instar	On diet A	On diet B	On diet C
Laboratory	3rd	100 ± 0 a	95 ± 3 a	100 ± 0 a
	4th	95 ± 3 a	100 ± 0 a	100 ± 0 a
	5th	100 ± 0 a	98 ± 2 a	97 ± 2 a
	6th	99 ± 1 a	99 ± 3 a	100 ± 0 a
Wild	3rd	100 ± 0 a	100 ± 0 a	100 ± 0 a
	4th	99 ± 1 a	100 ± 0 a	98 ± 2 a
	5th	98 ± 2 a	97 ± 2 a	97 ± 3 a
	6th	100 ± 0 a	100 ± 1 a	100 ± 0 a

Data in the table are represented as mean ± SE. Different lowercase letters following the data in the same column indicate significant difference at the 0.05 level (Tukey's test).

4 DISCUSSIONS

Cannibalism could facilitate the infection of certain pathogens that can be transmitted by feeding on infected conspecifics (Pfennig *et al.*, 1998; Pfennig, 2000; Williams and Hernández, 2006; Bolker *et al.*, 2008). This may have potential applications in the control of pests by entomopathogens to meet economic, public health, and environmental goals, and becomes the focus of several researches (Pfennig *et al.*, 1998; Pfennig, 2000; Williams and Hernández, 2006; Bolker *et al.*, 2008). Cannibalism of infected conspecifics can present two potential routes for the transmission of these pathogens: (1) wounds from defensive

responses by the cannibal's victim and (2) the consumption of massive doses of virus particles that may be sufficient to result in transmission. On one hand, the amount of pathogen particles is higher in older larvae. For example, infected 5th instar larvae of *S. frugiperda* with the mean weight of 35.1 ± 1.1 mg contained approximately $5 \times 1\ 010$ particles of invertebrate iridescent viruses, approximately 25% of the body weight of an infected insect comprises virus particles (Williams and Hernández, 2006). Similarly, instar had a marked effect on occlusion body production of a multiple nucleopolyhedrovirus. JHA-treated 6th instar larvae produced 4.8- and 5.6-fold increase in occlusion body production per dish compared with 5th instar at high and low densities, respectively (Elvira *et al.*, 2010). On the other hand, older larvae are more aggressive and voracious cannibals than younger ones. Thus, the cannibals ingested older larvae more frequently acquired the infection. In fact, 92% of *S. frugiperda* larvae that predated infected 5th instar conspecifics acquired the infection and died prior to adult emergence in the laboratory (Williams and Hernández, 2006).

Does the cannibal kill victims with larger body size than themselves? The only example has been documented in tadpoles (Crump, 1986) but not in insects. In the caterpillar *Litoprosopus futilis*, the opportunity to consume live conspecific is afforded only when the cannibals have larger body size than the victims (Semlitsch and West, 1988). Therefore, the ability of an insect species to cannibalize large victims at the same developmental stage is very important in the horizontal transmission of certain pathogens. In the present paper, we estimated the incidence of cannibalism of *H. armigera* larvae, with their cannibals and victims at the same developmental stage.

Our results showed that the cannibalism highly occurred in the 4th and 5th instars rather than the 3rd and 6th instars. Similarly, the incidence of cannibalism was significantly higher in the 5th instar compared with the 6th instar and increased with rearing density on both instars in *S. frugiperda* (Chapman *et al.*, 1999b; Elvira *et al.*, 2010). Moreover, the transmission of a granulovirus pathogen of the moth *P. interpunctella*, peaked in the middle (3rd and 4th) instars (Boots, 1998), indicating high incidence of cannibalism at this developmental stage.

Nutrition deficiency enhances cannibalism. In *S. frugiperda* and *M. brassicae* larvae, the frequency of cannibalism increased with decreasing food

quantity or quality (Vasconcelos, 1996; Chapman *et al.*, 1999b). *S. frugiperda* larvae feeding on sugarbeet foliage with low nitrogen content more frequently cannibalize beet armyworm pupae than those on sugarbeet foliage with normal and high nitrogen level (Al-Zubaidi and Capinera, 1983). *H. armigera* larvae fed on sodium-deprived artificial diet exhibited much more significant tendency in eating conspecific cadaver. However, in their study, the authors freshly incapacitated the victims by rupture of the head capsule to make them unable to injure cannibals (Xiao *et al.*, 2010). This result did not reflect the actual cannibalism in natural cotton fields. In the present paper, we confirmed the results of Xiao *et al.* (2010) using normal victims.

Since *S. frugiperda* cannibals exhibited some negative effects on larval development, such as the decreased survival and pupal weight, and reduced developmental rate (Chapman *et al.*, 1999a), we tested the influence of cannibalism and sodium deficiency in diet on pupation rates, and found that both of them had little effects.

We found that *H. armigera* larvae frequently cannibalize others with similar body size, and nutrition deficiency enhanced this behavior. Since many entomopathogens have excellent effects on *H. armigera* larvae (Dhandapani *et al.*, 1993; Wang *et al.*, 2010), some of these entomopathogens should be well horizontally transmitted by cannibalism under natural condition. The control effects of these entomopathogens in the cotton field is worthy of further researches.

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棉铃虫幼虫自相残杀习性与其龄期和食物营养的相关性

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摘要:【目的】昆虫自相残杀行为可以促进特定病原体的传播,这在利用昆虫病原体防治害虫方面有潜在的应用价值。本研究旨在探究棉铃虫 *Helicoverpa armigera* 幼虫自相残杀习性与其龄期及食物营养之间的相关性。【方法】分别饲喂室内品系和野外品系的棉铃虫幼虫含不同 Na⁺ 浓度的人工饲料,并在饲养至 3 龄、4 龄、5 龄和 6 龄时,将取食相同饲料的 10 头幼虫为一群组移入同一培养皿中,通过测定各处理幼虫存活率,评估幼虫龄期和饲料中的 Na⁺ 含量对自相残杀行为的影响。【结果】当以 3 龄和 4 龄为群组的起始龄期时,棉铃虫幼虫存活率显著低于起始龄期为 5 龄和 6 龄的群组。此外,取食正常人工饲料的幼虫存活率最高,取食缺钠饲料时,幼虫存活率明显下降。最后,幼虫群组起始龄期和食物 Na⁺ 含量对幼虫化蛹率无明显影响。【结论】结果说明,棉铃虫 4 和 5 龄幼虫与 3 和 6 龄幼虫相比,自相残杀行为发生的概率更大,而 Na⁺ 含量较低的食物在一定程度上促进自相残杀行为发生的可能性。本研究为在这一领域的进一步工作提供了基础。

关键词: 棉铃虫; 幼虫; 自相残杀; 幼虫龄期; 食物营养; 钠离子

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